Female-female mounting in the European rabbit

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Abstract

Mounting behaviour between adult females (FFM) was observed in experimental groups of previously unfamiliar female rabbits, housed in outdoor enclosures. Observations covered two periods: 1. the 1st week, when social organization was gradually being established (Phase 1), and 2. the 2nd and 3rd weeks, when social structure and dominance hierarchy were fully settled. FFM was more frequent in Phase 1 than in Phase 2, and was positively correlated with aggression (AG) in both Phases. Although the more aggressive females were higher in rank than less aggressive ones, no link was found between FFM and rank. The correlation between FFM and AG might thus depend on the fact that more aggressive females participated more in all forms of social interactions, including FFM. Analysis of dyads in Phase 2 revealed that the mounting females were usually dominant over the mountees. The frequent occurrence of FFM in unfamiliar rabbits suggests that it plays some role in the organization of social structures, although it does not seem to contribute directly to the establishment of dominance hierarchy. In addition, results indicate that once the rabbits are familiar with each other, FFM influences the dominance/subordination relationship, possibly by contributing to its maintenance and consolidation. Finally, the performance of FFM seems to be affected by contingent social conditions rather than by individual tendencies.

Introduction

Mounting between conspecific females (female-female mounting: FFM) has been reported in several mammals (see DAGG 1984 for an extensive review). Similar to the mounting of males by females, FFM has mainly been observed during the breeding season (Japanese macaques in particular, HANBY and BROWN 1974; WOLFE 1976; FEDIGAN and GOUZOULES 1978; GOUZOULES and GOY 1983), and in oestrous females (DAGG 1984; see also YOUNG 1961 on several species; FEDIGAN and GOUZOULES 1978 on Japanese macaques; FULKER-SON et al. 1983 in cattle). However, FFM has also been reported in non-reproductive and, more specifically, non-sexual contexts. Mounting behaviour is known to occur in anoestrous females in rabbits (YASCHINE et al. 1967), in dogs and some ungulates (DAGG 1984), and in rats (BEACH and RASQUIN 1942).

In oestrous females, FFM has generally been considered to be an aspect of female sexual behaviour (FEDIGAN and GOUZOULES 1978), possibly due to "sexual excitement" (HAM-MOND 1925, p. 70; DAGG 1984, p. 177). Unfortunately, this explanation sounds rather vague and says little about the causation and function of this behaviour.

Outside the sexual context, a link between FFM and aggression can be inferred from BERNSTEIN and MASON'S (1963) observations of the high rate of FFM and aggressive behaviours during the formation of a social group in Japanese macaques. FFM has also been reported to occasionally occur during aggressive interactions between unfamiliar rabbits (MYKYTOWYCZ and HESTERMAN 1973).

In primates (where FFM has probably been best studied) FFM has been suggested to favour the development of affinitive relationships between unrelated females (GOUZOULES and GOY 1983). Indeed, FAIRBANKS et al. (1977), working on rhesus monkeys, found that pairs of reciprocally mounting females consistently formed aggressive alliances against other females.

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Still in primates, an apparent correlation between FFM and social dominance has been found repeatedly (HINDE and ROWELL 1962; POIRIER 1970; DOYLE 1974; POIRIER and SMITH 1974; SEYFARTH 1976; STAMMBACH 1978).

Obviously, the function of FFM and its proximate causes may differ widely from species to species. Nevertheless, although the information on FFM at hand is fragmentary and at times even contradictory, it does seem possible that this behaviour may affect the formation and nature of social relationships between females.

In order to explore this possibility, we recorded the occurrence of FFM in groups of female domestic rabbits. Groups were formed experimentally from initially unfamiliar females. We expected FFM to be more frequent during the gradual organization of social structure and the reciprocal familiarization of the animals than later, when stable social structure had been fully established.

The correlation between FFM and aggression was also investigated. Finally, since social organization in female rabbits is characterized by a uni-sexual dominance hierarchy (MYERS and POOLE 1961), the possible relationship between FFM and individual rank was studied.

Materials and methods

Experimental conditions

Forty four female domestic rabbits (*Oryctolagus cuniculus L.*) were used, which came from a noninbred stock supplied by a local breeder. From birth to weaning, they had lived in cages with their mothers and litter-mates; at weaning, about 60 days after they were born, mothers and male littermates were removed. The study was started when the animals were approximately 100 days old; they were divided into 11 groups of four, including each unfamiliar subjects from four different litters, with similar body weight (mean weight 2.816 \pm 307 g). Each group was housed in an outdoor enclosure (4 × 4 m) with food and water ad libitum.

Procedure

Preliminary observations had revealed that when unfamiliar female rabbits are put into an unfamiliar environment, a brief period (usually two to three days) of intense activity, characterized by frequent agonistic interactions, is followed by a long lasting phase of low activity and apparently relaxed social interactions. Accordingly, observations focused on two distinct phases of behavioural organization:

- 1. Phase 1 an initial phase with unfamiliar animals (the females selected to form a group) newly introduced into an unfamiliar environment (the enclosure). Phase 1 observations began immediatly after the animals were introduced into the enclosure (day 1) and continued up to the fourth day, when social organization appeared fully established.
- 2. Phase 2 the following phase, when the animals were fully familiar with their group-mates and environment. Phase 2 observations took place during the second and third week of the animal's stay in the enclosure (days 8–10 and 21–23), when social organization appeared mostly stable.

stay in the enclosure (days 8–10 and 21–23), when social organization appeared mostly stable. Observations were carried out at dawn and dusk, when rabbits are known to be most active (MYKYTOWYCZ and ROWLEY 1958). In Phase 1, each group was observed for about one hour a day (mean daily observation time per group 65.5 min.). In Phase 2, each group was observed for a shorter period (mean daily observation time per group 43.4 min.), but for a greater number of days.

Behavioural items

For the purposes of this paper, female-female mounting (FFM), aggression (AG) and social activity (SA) were taken into consideration.

FFM includes mounting (clinging to the back of a conspecific with the forelegs and performing a series of pelvic thrusts) and attempts to mount (any attempt at mounting, which ended in failure to clasp the conspecific, usually because it moved away). These behaviours have already been described in female rabbits by HAMMOND (1925), BROOKS (1938), BEYER et al. (1964) and PALKA and SAWYER (1966), and by "cinematographic analysis". They were indistinguishable from the equivalent male behaviours (YASCHINE et al. 1967).

AG includes chasing, biting group-mates and hitting them with the hindlegs ("ripping" in MYKYTOWYCZ and HESTERMAN 1973; see also GRANT and MACKINTOSH 1963; FARABOLLINI 1987).

SA includes attending (orienting head, ears or whole body towards a conspecific); approaching

(moving towards a conspecific); nose-to-nose contact (touching the nose of a conspecific with nose); investigating (sniffing a conspecific's body); allo-grooming (grooming a conspecific); leaving (break-ing contact with a conspecific by quietly moving away; see GRANT and MACKINTOSH 1963). As the animals could be recognized individually by the colour patterns on their fur, both the

subject and the object of behaviours were recorded.

Every occurrence of each behaviour (ALTMANN 1974) was recorded on an EPSON microcomputer. The durations of the behaviours here in concern were too short to allow reliable recording. Consequently, we used frequency measures for statistical analysis.

Dominance hierarchy

The dominance or subordination of each individual in the dyadic relationship with each of its groupmates was assessed by computing a "subordination index (I)". Given two females, A and B, the subordination index of A in her relationship to B is computed as follows:

$$I_{A,B} = FL_{A,B}/AP_{B,A}$$
(1)

where $I_{A,B}$ is the subordination index of A in her relationship with B; $FL_{A,B}$ is the frequency of A's fleeing away from B; $AP_{B,A}$ is the frequency of B's approaching A. The higher the index, the higher the frequency with which A flees from B as B approaches. If the index of A is higher than that of B, then A is considered to be subordinate to B, and B is regarded as dominant over A (see for instance BERNSTEIN and SHARPE 1966).

The individual subordination index allowed us to assess the directionality of each dyadic dominance/subordination relationship between members of a given group. Hence, individuals could be ranked according to the number and identity of their subordinates, the top-ranking individual having the highest number of subordinates and the bottom-ranking individual none at all. To give an example, in group 4, Phase 1, female B was found to be dominant over females A, C and D; female D dominant over females A and C, female A over female C, and female C over none. The females were ranked accordingly in descending order B, D, A, C.

The linearity of dominance hierarchies was assessed using the Landau's index (h) for linearity (LEHNER 1979). Hereafter, whenever the females could be ranked in a linear order, they will be referred to as alpha (top-ranking female), beta (second), gamma (third) and omega (lowest in rank).

Dominance hierarchies were assessed separately for Phase 1 and Phase 2. They were also assessed a third time by further observations beginning seven days after Phase 2 had ended (ALBONETTI 1987). This third period of observation will be referred to as Phase 3. Its relevance for the purpose of this paper is solely concerned with the evaluation of concordance between hierarchies assessed at different times (see below).

Data analysis

Correlation between behaviours

The correlation between FFM, AG and SA in each Phase was assessed by computing the Spearman's correlation index (SIEGEL 1956).

Comparison between Phases

The frequencies of FFM, AG and SA respectively in Phase 1 and Phase 2 were compared by the twotailed Wilcoxon matched-pairs signed rank test (SIEGEL 1956).

Concordance between dominance hierarchies

The concordance between hierarchies in Phase 1, 2 and 3 was evaluated as follows:

Step 1. The animals and ranks in each group were each assigned a number from 1 to 4 (animal A = 1, animal D = 4; alpha = 1, omega = 4) for all three Phases. Taking group 4, Phase 1, again as an example, this gives:

animal	rank
B (2)	alpha (1)
D (4)	bêta (2)
A (1)	gamma (3)
C (3)	omega (4)

Step 2. For each group in each Phase, the Spearman correlation index was computed between the numbers assigned to the animals and the numbers assigned to rank, giving a series of 11 correlation indices for each Phase (one for each group).

Step 3. The Spearman correlation index was computed between the series of correlation indices for Phases 1 and 2, and those for Phases 2 and 3.

Comparison between ranks

The difference among behavioural frequencies recorded for individuals of different rank was evaluated by Friedman's non-parametric analysis of variance (StEGEL 1956). This analysis was carried out separatedly for FFM and AG; for Phase 1 and Phase 2; for individuals who performed (i.e., who were subject of) the behaviours and individuals who received (i.e., who were object of) them. Whenever a significant difference was found, ranks were compared using the two-tailed Wilcoxon signed rank test. Finally, hierarchial relationships between subjects and objects of FFM were analyzed in detail. The

Chi-square and two-tailed Binomial test (SIEGEL 1956) were used.

Results

Total observation times for each group and Phase are given in Table 1.

Correlation between behavioural items

A significant correlation was found between FFM, AG and SA in both Phases 1 and 2 (see Table 2 for significances).

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Table 1. Observation time per group per phase

Group	Observ	Observation time		
	Phase 1	Phase 2		
1	161 min.	263 min.		
2	240 min.	376 min.		
3	161 min.	264 min.		
4	204 min.	252 min.		
5	157 min.	258 min.		
6	222 min.	374 min.		
7	167 min.	245 min.		
8	175 min.	258 min.		
9	189 min.	279 min.		
10	310 min.	353 min.		
11	178 min.	261 min		
total	2.164 min.	3.183 min.		

Table 2	. Correla	ition	betwee	en ferr	1ale-f	emale
nountii	ng (FFM)	, aggr	ession	(AG)	and	social
	-	activit	y (SA)			

		Qs	Р	Ν
Phase 1	FFM vs AG	.296	= .05	44
	FFM vs SA	.482	< .001	44
	AG vs SA	.535	< .001	44
Phase 2	FFM vs AG	.360	< .02	44
	FFM vs SA	.309	< .05	44
	AG vs SA	.298	< .05	44

Comparison between Phases

FFM, AG and SA resulted significantly more frequent in Phase 1 than in Phase 2 (FFM, P = .044; AG, P < .001; SA, P < .001; Table 3).

Table 3. Female-female mounting (FFM), aggression (AG) and social activity (SA): comparison between Phases

	mean fr acts/hour	equency $(N = 44)$	Wilcoxon T	N	Р
FFM	Phase 1: Phase 2:	.579 .303	115	28	= .044
AG	Phase 1: Phase 2:	2.086 .358	94	37	< .001
SA	Phase 1: Phase 2:	16.062 12.246	216	44	< .001

Dominance hierarchy

The mean Landau's index for linearity of dominance hierarchy (h) per group was .963 in Phase 1 and .927 in Phase 2. As the lowest linearity threshold is h = .900 (LEHNER 1979), the dominance hierarchies may be regarded as linear.

A significant correlation was found between the dominance hierarchies in Phase 1 and Phase 2 ($\varrho_s = .695$, N = 11, P < .05) and in Phase 2 and Phase 3 ($\varrho_s = 0.88$, N = 11, P < .01).

Comparison between ranks

Individuals of different rank performed and received FFM with similar frequencies in either Phase (Table 4 and Fig. 1)

Individuals of different rank performed and received AG with significantly different frequencies (.02 < P < .01 and P < .05 respectively) in Phase 1, but not in Phase 2 (Table 5 and Fig. 2).

In Phase 1, AG was performed significantly more often by alpha females than by gamma (.01 < P < .02) and omega (P < .01) females, and by beta females significantly

Table 4. Female-female mounting (FFM): comparison among ranks by Friedman analysis of variance

	χ^2	df	Р
Phase 1: performed	.16	3	NS
received	.30	3	NS
Phase 2: performed	5.31	3	NS
received	1.20	3	NS

more often than by omega females (P = .02). Conversely, alpha females were significantly less often the object of AG than gamma (P < .01) and omega (P < .01) females (Table 6).

The analysis of pairs involved in FFM showed that in Phase 1 the number of dyads with the dominant partner acting as the performer and the subordinate as the recipient was not significantly different from that of dyads with the subordinate as the performer. However, in Phase 2 the

dominant-as-performer dyads were significantly more numerous than the other ones (P = .036; Table 7).

In both Phases 1 and 2 significantly fewer pairs were involved in reciprocal FFM (i.e., with both partners having the same probability of performing and receiving FFM) than in unidirectional FFM (with the same individual always playing the same role; Phase 1, P < .001; Phase 2, P = .008; Table 8).

Significantly fewer pairs were involved in FFM in both Phases (N = 6) than in one Phase only (N = 42; $\chi^2 = 27.00$; df = 1; p < .001).

When dyads where the dominant partner mounted the subordinate were considered, in Phase 1 mountings resulted significantly fewer where the dominant individual ranked immediatly above the subordinate (e.g., alpha females with beta, or beta with gamma), than in other combinations (P < .001). In other words, mountings were significantly fewer between individuals of adjacent rank than between individuals less distant in hierarchy. The opposite result was obtained in Phase 2 (P = .020; Table 9).

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		χ ²	df	Р
Phase 1:	performed received	10.80 7.98	3 3	.02 < P < .01 P < .05
Phase 2:	performed received	3.18 7.60	3 3	NS NS





N/h = number of acts per hour; rank 1 = alpha; rank 2 = beta; rank 3 = gamma; rank 4 = omega



Fig. 2. Frequencies of performed and received aggression (AG) by females of different rank in Phase 1 and Phase 2 respectively. Further details as in Fig. 1

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Finally, in Phase 1, 47.57 % of recorded FFMs was performed by the same individual (group 8 alpha female); 89.79 % of her mounting activity was directed towards the gamma female.

pairs of ranks	Wilcoxon T	N	Р	
		AG Performed		
alpha, beta	18	9	NS	
alpha, gamma	4	10	.01 < P < .02	alpha > gamma
alpha, omega	0	9	<.01	alpha > omega
beta, gamma	15	10	NS	
beta, omega	3	9	= .02	beta > omega
gamma, omega	17	11	NS	
		AG Received		
alpha, beta	10	9	NS	
alpha, gamma	0	9	< .01	alpha > gamma
alpha, omega	1	10	< .01	alpha > omega
beta, gamma	17	8	NS	
beta, omega	22	10	NS	
gamma, omega	11	10	NS	

Table 6. Phase 1, Aggression (AG): comparison between pairs of ranks

Table 7. Numbers of pairs with the dominant partner mounting the subordinate and vice versa

	mounting	g partner:	
	dominant	subordinate	
Phase 1 Phase 2	16 12	17 3	$\chi^2 = .03$ df = 1 NS Binomial test, p = .036

Table 8. Numbers of pairs involved in reciprocal and uni-directional female-female mountings (FFM)

FFM:	reciprocal	uni-directional	
Phase 1	5	28	$\chi^2 = 16.03 \text{ df} = 1 \text{ p} < .001$
Phase 2	2	13	Binomial test, p = .008

Table 9. Numbers of mountings directed by dominant individuals towards subordinate ones

pairs of individuals with:						
	adjacent rank	non-adjacent rank	χ^2	df		
Phase 1 Phase 2	21 39	53 21	13.83 5.40	1 1	p<.001 p=.020	

Discussion

The above findings provide new evidence on female-female mounting (FFM) occurring in the domestic rabbit even outside the breeding season. Under our experimental conditions, FFM was observed even though no males, or male cues of any kind, were present which could possibly favour the onset of reproductive activities (BRONSON 1974; CHEAL 1975). A positive correlation was found between FFM and aggression (AG) during the establishment of social structure in groups of initially unfamiliar females (Phase 1) and under stable social conditions (Phase 2). This correlation was more stringent in Phase 2 than in Phase 1.

Both FFM and AG were more frequent in Phase 1 than in Phase 2; the dramatic fall in AG in Phase 2 is particularly evident (Table 3 and Fig. 1).

A significant correlation was found between the dominance hierarchies in Phases 1 and 2, and in Phases 2 and 3. As a higher correlation index resulted between Phases 2 and 3 than between Phases 1 and 2, hierarchies were in better agreement in Phases 2 and 3 than in Phases 1 and 2. This suggested that changes in rank occurred between Phase 1 and 2, but not (or only in a minority of cases) between Phase 2 and 3. Therefore, hierarchies in Phase 2 were regarded as definitive, and animals were ranked according to them.

In Phase 1, females of different rank performed FFM with similar frequencies. However, the females which succeded in gaining the top ranks performed AG more frequently than lower ranking individuals. This result cannot be a mere by-product of the methods used to assess dominance hierarchies, since behaviours other than aggression were taken into account for this purpose.

In Phase 2, neither the frequencies of FFM or AG were dependent upon rank.

The positive correlation between FFM and AG and the higher frequency of these behaviours in Phase 1 than in Phase 2 suggest that they must be linked by a relationship (causal, functional, or both). However, similarities between FFM and AG go no further: in Phase 1, only the distribution of AG is affected by rank, not that of FFM.

The higher frequencies of AG in high-ranking females suggest that AG plays a role in the acquisition of social dominance. The marked fall in AG once the dominance hierarchy has been firmly settled (Phase 2) supports this hypothesis.

Contrary to AG, FFM does not seem to play a role in dominance acquisition, as no obvious relationship appears to exist between FFM and dominance hierarchy. It should be noted, however, that the opposite is true for male rabbits (FARABOLLINI 1987). In her study on four-male groups, the author reports frequent intra-sexual mountings by the dominant buck only.

Any possible connection between FFM and AG, suggested by their correlation and similar distribution in Phases 1 and 2, could simply depend on the fact that aggressive individuals generally tend to participate more in social interactions (agonistic and non-agonistic) than less aggressive ones (and vice versa). Indeed, FFM and AG were both highly correlated with social activity (SA), a large behavioural category including a number of different social, non-agonistic behaviours. In this respect, FFM could be seen as a social, presumably non-agonistic behaviour, whose correlation with AG depends on individuals being more or less interactive independently from the kind of social interaction itself. This hypothesis could also explain the different distribution of FFM in the two phases: its higher frequency in Phase 1 could depend on the fact that all social behaviours (including FFM and AG) are more frequent when the rabbits are familiarizing with each other and are building their social structures. Although FFM may not serve any specific function in the establishment of the dominance hierarchy, it can still provide information about conspecifics, e.g. through assessment of the reaction to approach and close physical contact, or detection of chemical signals, and thus act as a preliminary to more decisive interactions.

However, it would be premature at this stage to dismiss BERNSTEIN and MASON'S (1963) suggestion that FFM could simply be a behavioural consequence of "arousal due to novel situation" (p. 30), and that it serves no particular function in group formation.

If FFM does play a role in the familiarization with conspecifics, what possible function could it have in Phase 2, when the animals are fully familiar with each other? In other words, why is there no dramatic fall in FFM as there is in AG in Phase 2?

Since the establishment of rank order within the group did not seem to provide the

answer to the problem of the function of FFM, attention was focused on the partners involved in FFM, and the dominance/subordination relationship between them was investigated. The directionality of diadic dominance relationships did not appear to influence FFM in Phase 1, when the process of dominance acquisition in diadic relationships themselves was taking place. In Phase 2, however, once dominance was apparently fully established, the mounting female was usually dominant over the mountee. This suggests that, under stable social conditions, FFM could be aimed at confirming and consolidating dominance in diadic relationships. It must be stressed that FFM need not necessarily have the same functional significance, if any, during the development of social organization and under stable social conditions.

As an additional comment, one of the females (A8) performed FFM extremely frequently in Phase 1. This observation seems to support HANBY and BROWN'S (1974) suggestion that FFM can represent an individual peculiarity (see also YASCHINE et al. 1967). In this instance, however, as A8 almost always mounted one and the same groupmate (C8), FFM seemed to be a characteristic of a given diadic relationship rather than of a given individual. In Phase 2, A8 did not show any behavioural peculiarity. This observation, together with the fact that the same individuals rarely performed FFM in both Phases 1 and 2, suggests that the tendency to engage in FFM is influenced more by the social context than by individual propensities.

Reciprocal FFM ist extremely rare, which indicates the uni-directional nature of this behaviour in female rabbits and supports the hypothesis of a link between FFM and dominance in diadic relationships. On the other hand, FFM never appears to have an affiliative function by strengthening social bonds between two reciprocally mounting females, as seems to be the case in some Primates (FAIRBANKS et al. 1977; GOUZOULES and Goy 1983).

As a final point, since rabbits are reported to ovulate as a result of mounting and even in the absence of intromission (HAMMOND 1925; FEE and PARKES 1930), FFM might cause ovulation in the mounted female. Infertile ovulation is usually followed by pseudopregnancy (HAMMOND 1925) and consequently the mounted female could suffer prolonged delay in reproduction. FFM could thus decrease reproductive success in conspecific females, and be one of the possible determinants of differential reproductive success in female rabbits. Further investigation is needed to clarify the actual effectiveness of female mounting as a stimulus inducing ovulation, and to evaluate the neuro-endocrinal consequences of this behaviour in the mounting and the mounted female.

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Zusammenfassung

Aufreitversuche zwischen weiblichen europäischen Kaninchen

Die vorliegende Verhaltensstudie befaßt sich mit Aufreitversuchen zwischen weiblichen Kaninchen (female-female mounting = FFM). Zum Zweck unseres Experimentes wurden Versuchsgruppen von weiblichen, untereinander fremden Kaninchen in einem Freigelände eingesperrt und über zwei Zeiträume hin beobachtet: 1) während der ersten Woche nach der Einsperrung, als sich so langsam eine Sozialordnung herauskristallisierte (Phase 1) und 2) während der zweiten und dritten Woche, als die Sozialordnung und die Hierarchie feststanden. Während Phase 1 konnten mehr FFM beobachtet werden als in Phase 2, wobei FFM in beiden Phasen mit Aggression (AG) verbunden war. Vom hierarchischen Standpunkt her kann davon ausgegangen werden, daß die aggressiveren Weibchen die ranghöheren Positionen belegen. Allerdings konnte kein direkter Zusammenhang zwischen FFM und AG festgestellt werden. Die Verbindung von FFM und AG mag allenfalls darin liegen, daß die

aggressiveren Weibchen intensiver an jeder Art von sozialer Interaktion beteiligt sind, und demnach auch an FFM. In der zweiten Phase vorgenommene Paaranalysen haben ergeben, daß die aufreitenden Weibchen gewöhnlich über die aufgerittenen Weibchen dominieren. Das häufige Auftauchen von FFM bei untereinander fremden Weibchen mag darauf hinweisen, daß FFM eine Rolle bei der Organisation der Sozialstrukturen spielt, auch wenn es wahrscheinlich keinen direkten Einfluß auf die Festlegung der Hierarchie ausübt. Unsere Beobachtungen ergeben auch, daß FFM bei Kaninchen, die sich nicht mehr fremd sind, die Über- und Unterordnung beeinflußt und sich möglicherweise auf ihre Beibehaltung und Verstärkung auswirkt. Das Auftreten von FFM scheint eher von zufälligen sozialen Voraussetzungen beeinflußt zu sein als von individuellen Tendenzen.

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